

# The adaptive significance of host location by vibrational sounding in parasitoid wasps

Gavin R. Broad<sup>1,2</sup> and Donald L. J. Quicke<sup>2,3\*</sup>

<sup>1</sup>Centre for Population Biology, and <sup>2</sup>Unit of Parasitoid Systematics, CABI Bioscience UK Centre (Ascot), Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK

<sup>3</sup>Department of Entomology, The Natural History Museum, London SW7 5BD, UK

Vibrational sounding, which is a form of echolocation, is a means of host location by some parasitoid wasps. The wasp taps the substrate (wood, stem or soil) and detects the position of a potential host through the returning 'echoes'. The deployment of vibrational sounding is inferred through the form of the subgenual organ in the female tibia in combination with the presence of modifications to the female antenna used for tapping the substrate. Vibrational sounding and its associated modifications were found in two families. The use of vibrational sounding by parasitoid wasps was positively correlated with the depth of the host in the substrate relative to the size of the parasitoid. There were also significant correlations between the use of vibrational sounding and parasitism of immobile and concealed hosts and between vibrational sounding and idiobiosis. The data suggested that vibrational sounding evolved under a variety of ecological conditions, being employed in the location of wood-boring, stem-boring, soil-dwelling and cocooned hosts and stem-nesting aculeates, often in situations in which the host does not produce vibrations itself.

**Keywords:** Hymenoptera; echolocation; comparative method; host shifts

## 1. INTRODUCTION

Interpreting the adaptive significance of a trait can be achieved through experimentation or correlation (Williams 1992). Here we integrate these methodologies using phylogenies of the Hymenoptera, together with the results of published experimental work on a limited number of species, so as to infer which ecological conditions have promoted the evolution of an unusual method of host location, i.e. vibrational sounding.

Studies aimed at elucidating the historical processes underlying the diversity of host use patterns of parasitic wasps have focused primarily on broad-scale factors such as host taxon and habitat type (e.g. Shaw 1983, 1988; Gauld 1988). Another approach is to examine some of the more mechanistic, wasp-level factors that have played a role in generating host range. One such factor is the method of host location employed. Although the mechanics of host location are only understood for a minority of hymenopteran taxa, a comparative approach towards the evolution of host location mechanisms in different taxa should make a more holistic explanation of patterns of shifts in host range emphasis possible. Here we take a step towards this aim by examining the distribution and ecology of one form of host location. The use of vibratory cues emanating from potential hosts is well documented in parasitoid wasps (Meyhöfer & Casas 1999). However, the use of self-produced vibrational signals, i.e. echolocation via a solid medium, in detecting hosts is less well understood, having only been demonstrated for two species of the ichneumonid genus *Pimpla*, both of which are idiobiont endoparasitoids of cocooned Lepidoptera pupae (Henaut & Guerdoux 1982; Wäckers *et al.* 1998).

The use of vibrational sounding can be inferred by examining external morphology. The wasps produce pulses of sound by tapping the substrate with their antennae (Henaut 1990; Otten *et al.* 2000) and then detect the echoes with particularly enlarged subgenual organs in the legs (Vilhelmsen *et al.* 2001). These may contain approximately 400 vibration-detecting scolopale cells per organ (Vilhelmsen *et al.* 2001) compared with 3–50 in most insects (Menzel & Tautz 1994) and are externally obvious as swollen and clavate tibiae. The antennae bear hardened modifications which may take the form of 'hammers', pegs or thickenings of the apical flagellomeres with projections (figure 1) (Gauld 1997; Wahl & Gauld 1998; Vilhelmsen *et al.* 2001). Further, the subgenual organ in taxa that use vibrational sounding is enlarged in females only, and only females have modifications to the antennae associated with tapping a substrate. Parasitoids that are known to rely upon the host's vibratory cues rather than vibrational sounding for detecting their hosts have neither enlarged subgenual organs nor antennal modifications.

We have established the phylogenetic distribution of vibrational sounding across the Hymenoptera and tested for factors that may explain its distribution. We predict the evolution of vibrational sounding to be associated with the parasitism of deeply concealed hosts and, in particular, of immobile hosts such as pupae. Further, since it is a fairly indiscriminate form of host location (Halstead (1987) reported on an example of attempted oviposition into bean seeds), we hypothesize that, if this was the primary means of host location, it would be correlated with idiobiosis, i.e. parasitoids that do not allow the host to grow or metamorphose beyond the stage attacked (Askew & Shaw 1986). In contrast, koinobiont parasitoids, which allow the host to develop further following parasitism and which typically have more intimate physiological interactions with their hosts

\*Author for correspondence (d.quicke@ic.ac.uk).

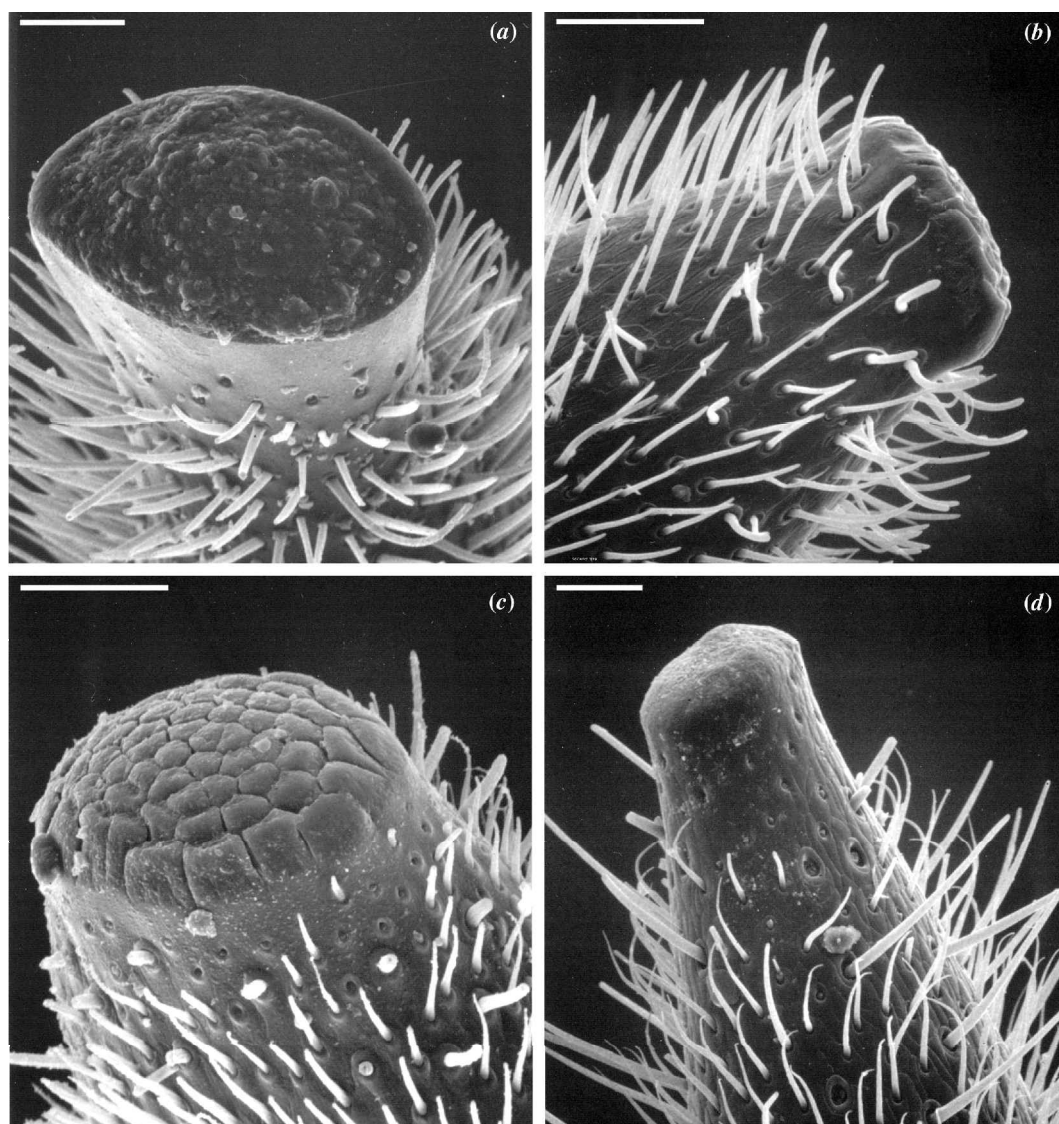


Figure 1. Antennae of (a) *Echthrus reluctator* (Linn.), (b) *Xoridesopus* sp., (c) *Schreineria* sp. (Ichneumonidae: Cryptinae), and (d) *Labena schausi* Cushman (Ichneumonidae: Labeninae), showing the highly modified tips used for beating the substrate. Scale bar, 50  $\mu$ m.

(Mayhew & Blackburn 1999), would be expected to rely on more discriminating clues as to the identity of the potential host.

## 2. MATERIAL AND METHODS

### (a) *Measurements*

Female wasps were interpreted as using vibrational sounding by the presence of both relatively enlarged and clavate tibiae, indicating the presence of an enlarged subgenual organ, and an antennal modification (as described in § 1), the shapes of which differ clearly from the unspecialized forms found in the males. In a few taxa, e.g. Gasteruptionidae and Peradeniidae, both sexes possess grossly expanded and clavate hind tibiae. It is assumed that, if this is a hypertrophied subgenual organ, then it is not swollen solely for reasons of host location because males do not detect hosts. Females of a few taxa possess swollen tibiae but not antennal modifications; these are presumed not to be using vibrational sounding.

The degree of subgenual organ development was expressed as the absolute intersexual difference in the ratio of the length to

the breadth of the fore tibia. For the ichneumonid subfamily Xoridinae, all members of which appear to use vibrational sounding, subgenual organ development was measured on the fore, mid and hind legs for a range of species of different ovipositor length.

Body length was measured from the anterior edge of the eyes to the tip of the metasoma. Ovipositor length was measured at the maximum extrusion. The relative depth of the host, the 'ovipositor proportion', was defined as the length of the exposed ovipositor divided by the length of the body. Taxa were scored according to (i) whether their hosts are concealed or not, (ii) idiobiosis, (iii) immobility of the host at the time of parasitism, and (iv) type of host substrate (wood or soil). Measurements for the rare proctotrupoid *Peradenia clavipes* were taken from Naumann & Masner (1985).

### (b) *Phylogeny construction*

One hundred and thirty-seven exemplar species were chosen from as wide a taxonomic and biological range as possible. In the course of this study we examined 55 of the 58 parasitoid families (with data for one further family extracted from the

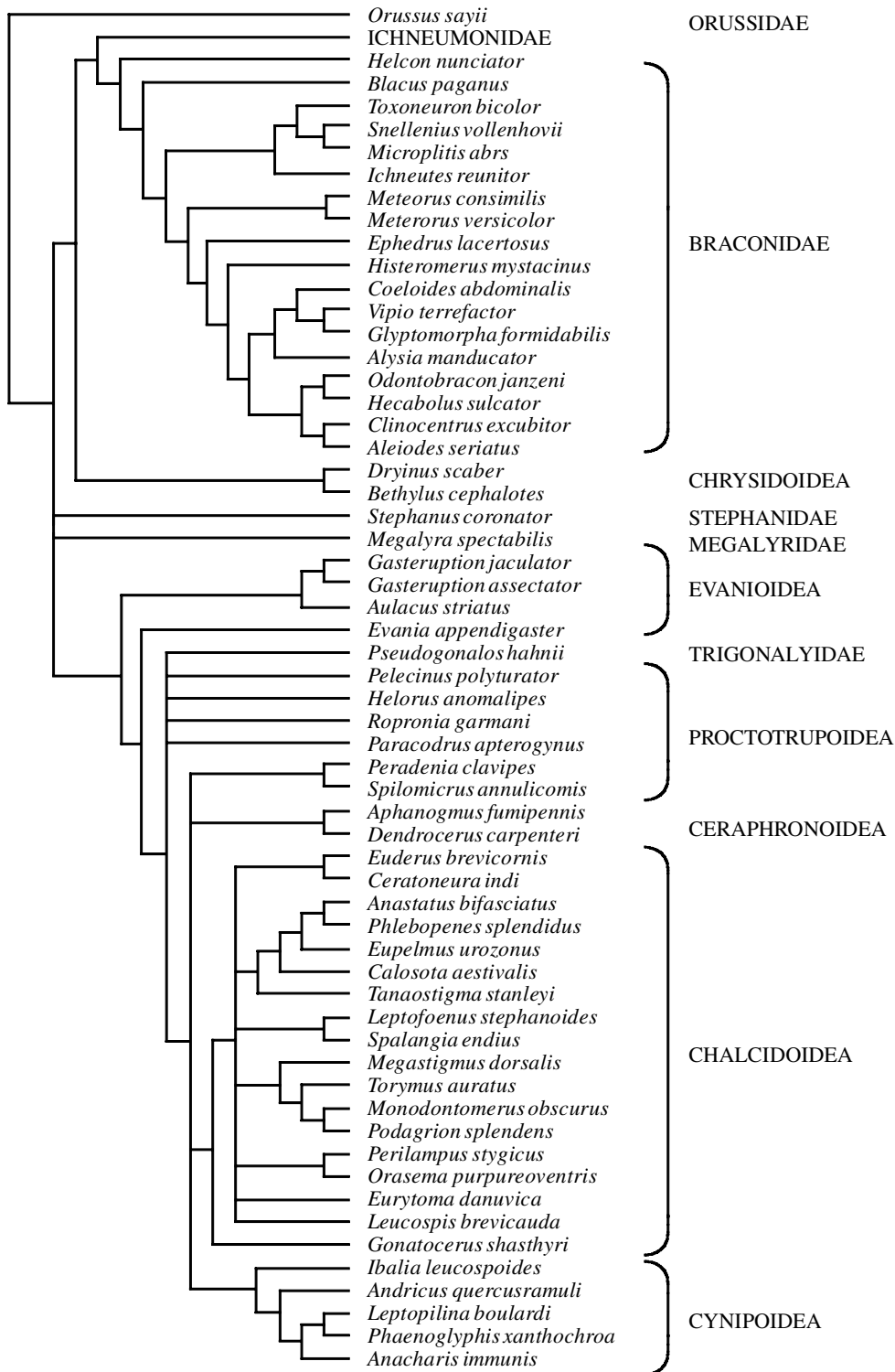


Figure 2. Phylogeny of the hymenopteran species (Ichneumonidae excluded) used in the comparative analyses. Compiled from Gibson (1995), Grissell (1995), Ronquist (1995), Belshaw *et al.* (1998) and Basibuyuk *et al.* (2001).

literature) for evidence of vibrational sounding of hosts. Emphasis was placed on the Ichneumonidae, where vibrational sounding seemed to be most prevalent, with approximately 800 genera examined.

The phylogeny of the Hymenoptera used for the mapping of traits and for the comparative analyses (see §2(c)) (figures 2 and 3) was taken from Basibuyuk *et al.* (2001) at the family level. Basibuyuk *et al.* (2001) is a reanalysis of Rasnitsyn's (1988) data with the inclusion of more recent character systems (data set available at <http://www.bio.ic.ac.uk/research/dlq/>

[matrix.pau](http://www.bio.ic.ac.uk/research/dlq/matrix.pau)). The phylogeny of the Ichneumonidae (figure 3) was taken from Quicke *et al.* (2000) with further resolution from various sources (Townes 1969; Wahl & Gauld 1998; Gauld & Wahl 2000; Gauld *et al.* 2001). All of the xoridine species groups of Wahl (1997) were measured for tibial dimensions and ovipositor size. A phylogenetic picture of the very large superfamily Chalcidoidea is a fanciful concept at present. Inclusion of many more taxa in a taxonomic hierarchy would have been uninformative or misleading as many of the higher taxa are evidently para- or polyphyletic (LaSalle *et al.* 1997; Gibson *et al.* 1999).

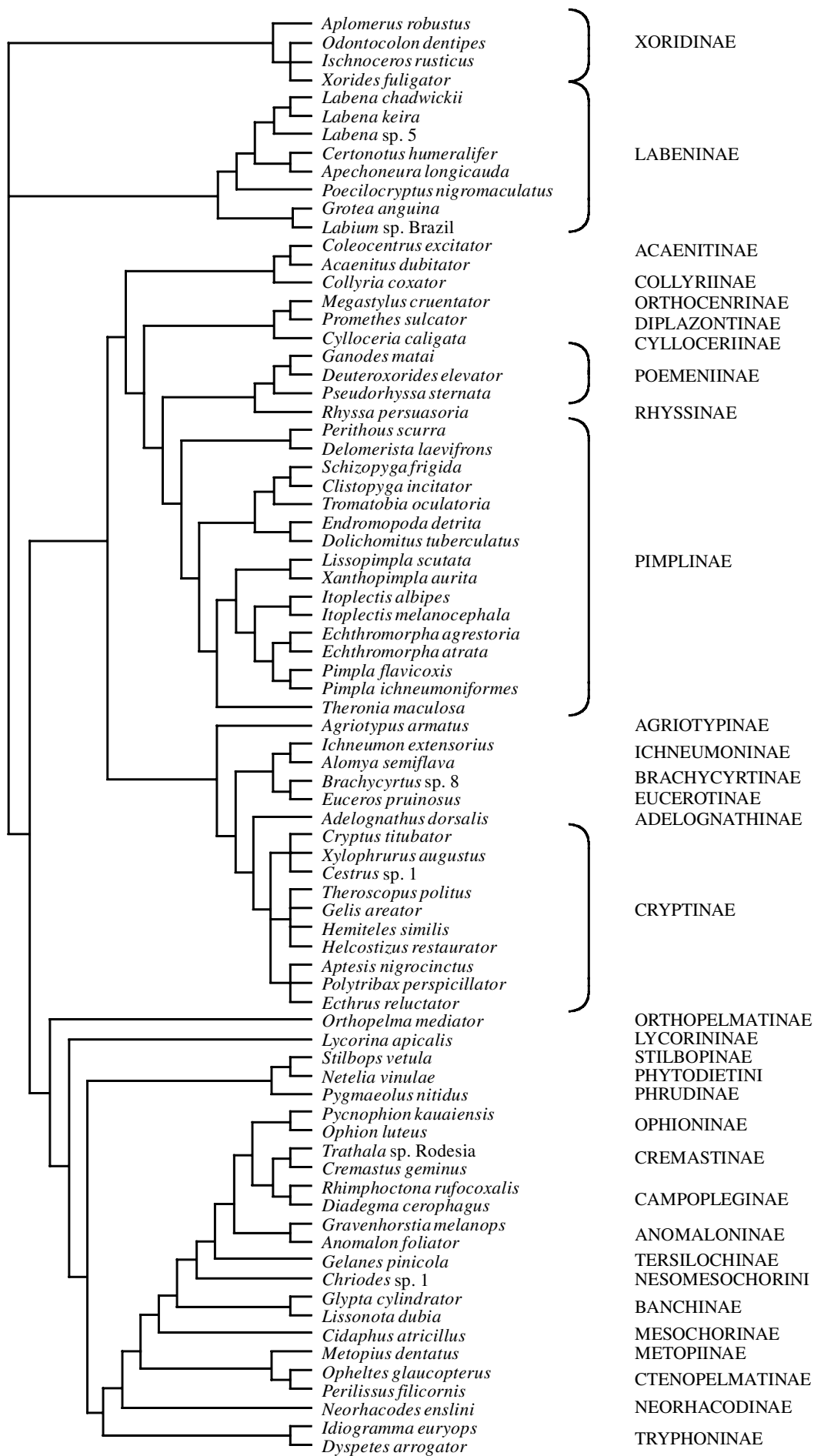


Figure 3. Phylogeny of the ichneumonid species used in the comparative analyses.

Table 1. *Taxonomic distribution of taxa manifesting an enlarged subgenual organ and modified antenna tips*

(Austroiniidae, Renyxiidae and Monomachidae (Proctotrupoidea) were not included in the analyses due to lack of comparative male and female material.)

superfamily (number of families included) family (number of subfamilies and genera included) subfamily (number of genera included) tribe (number of genera included)	genera/species with enlarged female subgenual organs and antennal modifications
Orussoidea (one) Orussidae (two and 16)	all species
Ichneumonoidea (two) Ichneumonidae (39 and 2870)	
Xoridinae (four)	all species
Labeninae (12)	all species of <i>Labena</i>
Cryptinae (379) Phygadeuontini (120)	<i>Bilira</i> and <i>Helcostizus</i> , plus several undetermined species, including a genus near <i>Phygadeuon</i>
Hemigasterini (25)	<i>Echthrus</i>
Cryptini (204)	many genera
Claseinae (two) ( <i>sensu</i> Porter 1998)	<i>Ephysis</i> ; included as a tribe in Cryptinae by Gauld (1983)
Pimplinae (66) Pimplini (nine)	many species of <i>Pimpla</i> and <i>Itopectis</i> and at least one species of <i>Echthromorpha</i>

### (c) *Comparative analyses and phylogenetic independence*

The program Comparative Analysis using Independent Contrasts (CAIC) (Purvis & Rambaut 1995) was used in order to test for correlations involving at least one continuous character. Regressions for two continuous characters were carried out on the independent contrasts, with the regression line forced through the origin. A one-tailed *t*-test was performed on the contrasts for one continuous and one categorical variable in order to test whether the dependent variable increased in the same direction as the independent variable (that is, whether the mean of the contrasts significantly differed from zero). Independent contrasts methods are not applicable to tests of two categorical variables. Maddison's (1990) concentrated changes test, as implemented in MacClade (Maddison & Maddison 1992), was used for testing for correlated evolution of two categorical variables. As the test requires that the tree be strictly bifurcating and our phylogenies contained polytomies, each test was performed on ten random, completely bifurcating resolutions of the phylogeny. A potential problem with this method is that large, uniform blocks of taxa make the results of the test more likely to be significant (Sillén-Tullberg 1993; Grafen & Ridley 1997). In order to circumvent this problem we pruned sections of the tree where the taxa were uniform for both characters being tested down to one exemplar species. This resulted in a very conservative test of association. The results are reported with *n* as the number of gains of the dependent variable on branches of the tree where there were gains in the independent variable. The range of probabilities using ten random resolutions of the phylogeny is given.

## 3. RESULTS

### (a) *Phylogenetic distribution*

Vibrational sounding for hosts, as inferred by the presence of both an enlarged subgenual organ and antennal modifications in the female, was found in only two out of 56

parasitoid hymenopteran families examined. All members of the putatively most basal parasitoid family, the Orussidae (Gibson 1985, 1993; Whitfield 1992; Villhelmsen 1997), possess these characters, as do five out of approximately 39 subfamilies of the Ichneumonidae (table 1).

The use of vibrational sounding was parsimoniously reconstructed to have evolved on seven occasions (the Claseinae were not included in the comparative analyses due to conflicting opinions on their systematic position within the Ichneumonidae). However, further phylogenetic resolution of the ichneumonid subfamilies Pimplinae and Cryptinae may reveal that the use of vibrational sounding has evolved on more occasions.

### (b) *Correlates of vibrational sounding*

Vibrational sounding modifications were positively correlated with (i) the presence or absence of host concealment ( $n = 9$  and  $p = 0.009\text{--}0.019$ ), (ii) the relative depth of concealment (d.f. = 21,  $t = 3.66$  and  $p < 0.001$ ), (iii) parasitoid idiobiosis ( $n = 6\text{--}7$  and  $p = 0.001\text{--}0.025$ ), and (iv) the parasitism of immobile host stages (not including eggs) ( $n = 7$  and  $p < 0.001\text{--}0.001$ ). There was no significant correlation across the vibrational sounding Hymenoptera as a whole between the degree of subgenual organ development and the relative depth of the host (d.f. = 15,  $F = 4.12$  and  $p = 0.062$ ). This latter result was duplicated for the sizes of the subgenual organs of the fore, mid and hind legs of xoridine ichneumonids (d.f. = 16,  $F < 0.001\text{--}0.56$  and  $p = 0.465\text{--}0.964$ ) at a narrower taxonomic scale. There was no significant correlation between host substrate and the use of vibrational sounding (wood substrate,  $n = 4$  and  $p = 0.062\text{--}0.096$ , and soil substrate,  $n = 3$  and  $p = 0.370\text{--}0.430$ ). Vibrational sounding taxa included parasitoids of wood-boring beetles and wood wasps, stem-nesting Hymenoptera, stem-boring Lepidoptera and Hymenoptera, cocooned Lepidoptera pupae and soil-dwelling Diptera.

#### 4. DISCUSSION

The results supported our hypotheses that enlarged subgenual organs and antennal modifications are positively correlated with greater relative host depth, immobility of the host and idiobiosis. Vibrational sounding was only found in certain members of two families out of approximately 58 parasitoid families. Notably, no taxa exhibiting the outward manifestations of vibrational sounding were found within the biologically and numerically hugely diverse superfamily Chalcidoidea. The data suggested that analogous adaptations to vibrational sounding evolved under a variety of ecological conditions, being employed in the location of wood-boring, stem-boring, soil-dwelling and cocooned hosts and stem-nesting aculeates, as a means of detecting immobile host stages in concealment.

The method employed here for testing whether or not two discrete characters are correlated (Maddison 1990) required knowledge of the number of occasions the trait of interest has evolved and been lost. Parsimony reconstructions showed vibrational sounding to have evolved on seven occasions. The uncritical use of parsimony may not always be the best method of reconstructing ancestral character states accurately if there is an unequal probability of gains and losses (Cunningham *et al.* 1998). The possibility exists that vibrational sounding was a feature of early parasitoids, which was then lost in many lineages as they exploded in diversity, as many of those taxa employing vibrational sounding occupy rather basal branches of the hymenopteran tree (i.e. Orussidae as the sister group to the rest of the parasitoid Hymenoptera (Gibson 1985, 1993; Whitfield 1992; Vilhelmsen 1997) and Xoridinae and Labeninae as basal ichneumonid subfamilies (Quicke *et al.* 1999)). More complete phylogenetic pictures of the groups involved should enable us to determine the number of evolutions of vibrational sounding more accurately.

Much speculative work concerning the evolution of host range emphasis has assumed the general applicability of Gauld's (1988) hypotheses of host use in ichneumonoids (e.g. Whitfield 1998), i.e. that parasitoids have followed hosts from deep concealment to loose concealment to exposure, with major life-history alterations being associated with shifts in host stage and host exposure. This assumption is called into question by the knowledge that some ichneumonid groups use vibrational sounding. To some extent, the patterns of host use observed within the Ichneumonidae are likely to have been dependent upon the constraints and opportunities arising from the use of vibrational sounding by taxa that are idiobionts and attacking concealed, immobile hosts. Some of the differences observed in reproductive biology within the Ichneumonidae can also be explained by the use of vibrational sounding, for example amongst parasitoids of wood-boring hosts there is a much higher success rate in contacting hosts of *Xorides brachylabris*, which uses vibrational sounding, when compared to *Rhyssa persuasoria*, which does not (Chrystal & Skinner 1931). The advantages of accurate host location are obvious when one considers the efforts of these wasps, drilling through several centimetres of wood whilst being exposed to considerable predation pressure (Quicke 1997). However,

there is no evidence at present as to why some taxa employ this method of host location and why some do not.

We have demonstrated the adaptive significance of two traits involved in the location of deeply concealed immobile hosts by vibrational sounding using a comparative method. We now need more information on the host location mechanisms employed by other parasitoids of deeply concealed hosts in order to understand the role that host location plays in generating host range.

We thank David Wahl at the American Entomological Institute (Gainesville) who allowed specimens in his care to be used for measurements and Hasan Basibuyuk for the scanning electron micrographs of antenna tips. Rob Belshaw and Konrad Dolphin provided much fruitful and, occasionally, fruitless discussion and comment. Mike Fitton's constructive criticism is appreciated and Nicola Ti  n made helpful comments on some of the many drafts of the manuscript. Gavin Broad was supported by a Natural Environment Research Council studentship.

#### REFERENCES

- Askew, R. R. & Shaw, M. R. 1986 Parasitoid communities: their size, structure and development. In *Insect parasitoids* (ed. J. Waage & D. Greathead), pp. 225–264. London: Academic Press.
- Basibuyuk, H. H., Vilhelmsen, L., Rasnitsyn, A. P. & Quicke, D. L. J. 2001 Phylogeny of the Hymenoptera (Insecta): a reanalysis of Rasnitsyn's (1988) data set with the inclusion of more recent character systems. (In preparation.)
- Belshaw, R., Fitton, M. G., Herniou, E., Gimeno, C. & Quicke, D. L. J. 1998 A phylogenetic reconstruction of the Ichneumonoidea (Hymenoptera) based on the D2 variable region of 28S ribosomal RNA. *Syst. Entomol.* **23**, 109–123.
- Chrystal, R. N. & Skinner, E. R. 1931 Studies in the biology of *Xylonomus brachylabris* Kr., and *X. irrigator* F., parasites of the larch longhorn beetle, *T  tropsium gabrieli* Weise. *Forestry* **5**, 21–33.
- Cunningham, C. W., Omland, K. E. & Oakley, T. H. 1998 Reconstructing ancestral character states: a critical reappraisal. *Trends Ecol. Evol.* **13**, 361–366.
- Gauld, I. D. 1983 The classification, evolution and distribution of the Labeninae, an ancient southern group of Ichneumonidae (Hymenoptera). *Syst. Entomol.* **8**, 167–178.
- Gauld, I. D. 1988 Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biol. J. Linn. Soc.* **35**, 351–377.
- Gauld, I. D. 1997 Ichneumonidae of Costa Rica, 2. *Mem. Am. Entomol. Inst.* **57**, 1–485.
- Gauld, I. D. & Wahl, D. B. 2000 The Labeninae (Hymenoptera: Ichneumonidae): a study in phylogenetic reconstruction and evolutionary biology. *Zool. J. Linn. Soc.* **129**, 271–347.
- Gauld, I. D., Wahl, D. B. & Broad, G. R. 2001 A phylogenetic reconstruction of the Pimplinae (Hymenoptera: Ichneumonidae). (In preparation.)
- Gibson, G. A. P. 1985 Some pro- and mesothoracic characters important for phylogenetic analysis of Hymenoptera, with a review of terms used for structures. *Can. Entomol.* **117**, 1395–1443.
- Gibson, G. A. P. 1993 Groundplan structure and homology of the pleuron in Hymenoptera based on a comparison of the skeleto-musculature of Xyelidae (Hymenoptera) and Raphidiidae (Neuroptera). *Mem. Entomol. Soc. Can.* **165**, 165–187.
- Gibson, G. A. P. 1995 Parasitic wasps of the subfamily Eupelminae: classification and revision of world genera (Hymenoptera: Chalcidoidea: Eupelmidae). *Mem. Entomol. Int.* **5**, 1–421.



- Gibson, G. A. P., Heraty, J. M. & Woolley, J. B. 1999 Phylogenetics and classification of Chalcidoidea and Mymarommatoidea—a review of current concepts (Hymenoptera, Apocrita). *Zool. Scripta* **28**, 87–124.
- Grafen, A. & Ridley, M. 1997 A new model for discrete character evolution. *J. Theor. Biol.* **184**, 7–14.
- Grissell, E. E. 1995 Toryminae (Hymenoptera: Chalcidoidea: Torymidae): a redefinition, generic classification, and annotated world catalog of species. *Mem. Entomol. Int.* **2**, 1–470.
- Halstead, A. J. 1987 Unusual behaviour by *Pimpla instigator* (F.) (Hym., Ichneumonidae). *Entomol. Mon. Mag.* **123**, 189.
- Henaut, A. 1990 Study of the sound produced by *Pimpla instigator* (Hymenoptera: Ichneumonidae) during host selection. *Entomophaga* **35**, 127–139.
- Henaut, A. & Guerdoux, J. L. 1982 Location of a lure by the drumming insect *Pimpla instigator*. *Experientia* **38**, 346–347.
- LaSalle, J., Polaszek, A., Noyes, J. S. & Zolnerowich, G. 1997 A new whitefly parasitoid (Hymenoptera: Pteromalidae: Eunotinae), with comments on its placement, and implications for classification of Chalcidoidea with particular reference to the Eriaporinae (Hymenoptera: Aphelinidae). *Syst. Entomol.* **22**, 131–150.
- Maddison, W. P. 1990 A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557.
- Maddison, W. P. & Maddison, D. R. 1992 *MacClade: analysis of phylogeny and character evolution*, v. 3.04. Sunderland, MA: Sinauer Associates.
- Mayhew, P. J. & Blackburn, T. M. 1999 Does development mode organize life-history traits in the parasitoid Hymenoptera? *J. Anim. Ecol.* **68**, 906–916.
- Menzel, J. G. & Tautz, J. 1994 Functional morphology of the subgenual organ of the carpenter ant. *Tissue Cell* **26**, 735–746.
- Meyhöfer, R. & Casas, J. 1999 Vibratory stimuli in host location by parasitic wasps. *J. Insect Physiol.* **45**, 967–971.
- Naumann, I. D. & Masner, L. 1985 Parasitic wasps of the proctotrupoid complex: a new family from Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). *Aust. J. Zool.* **33**, 761–783.
- Otten, H., Wäckers, F. L., Battini, M. & Dorn, S. 2000 Efficiency of vibrational sounding in the parasitoid *Pimpla turionellae* is affected by female size. *Anim. Behav.* (In the press.)
- Porter, C. C. 1998 Guía de los géneros de Ichneumonidae en la región Neártica del sur de Sudamérica. *Op. Lilloana* **42**, 1–234.
- Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.
- Quicke, D. L. J. 1997 *Parasitic wasps*. London: Chapman & Hall.
- Quicke, D. L. J., Lopez-Vaamonde, C. & Belshaw, R. 1999 The basal Ichneumonidae (Insecta: Hymenoptera): 28S D2 rDNA considerations of the Brachycyrtinae, Labeninae, Paxylommatainae and Xoridinae. *Zool. Scripta* **28**, 203–210.
- Quicke, D. L. J., Fitton, M. G., Notton, D. G., Broad, G. R. & Dolphin, K. 2000 Phylogeny of the Ichneumonidae (Hymenoptera): a simultaneous molecular and morphological analysis. In *Hymenoptera: evolution, biodiversity and biological control* (ed. A. D. Austin). Canberra: CSIRO Publishing.
- Rasnitsyn, A. P. 1988 An outline of the evolution of the hymenopterous insects (order Vespida). *Orient. Insects* **22**, 115–145.
- Ronquist, F. 1995 Phylogeny and early evolution of the Cynipoidea (Hymenoptera). *Syst. Entomol.* **20**, 309–335.
- Shaw, M. R. 1983 On[e] evolution of endoparasitism: the biology of some genera of Rogadinae (Braconidae). *Cont. Am. Entomol. Inst.* **20**, 307–328.
- Shaw, S. R. 1988 Euphorine phylogeny: the evolution of diversity in host-utilization by parasitoid wasps (Hymenoptera: Braconidae). *Ecol. Entomol.* **13**, 323–325.
- Sillén-Tullberg, B. 1993 The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. *Evolution* **47**, 1182–1191.
- Townes, H. K. 1969 Genera of Ichneumonidae, part 2. *Mem. Am. Entomol. Inst.* **12**, 1–537.
- Vilhelmsen, L. 1997 The phylogeny of lower Hymenoptera (Insecta), with a summary of the early evolutionary history of the order. *J. Zool. Syst. Evol. Res.* **35**, 49–70.
- Vilhelmsen, L., Isodoro, N., Bin, F., Basibuyuk, H. H. & Quicke, D. L. J. 2001 Host location and oviposition in a basal parasitic wasp family: the subgenual organ, ovipositor, and associated structures of the Orussidae (Hymenoptera, Insecta). (In preparation.)
- Wäckers, F. L., Mitter, E. & Dorn, S. 1998 Vibrational sounding by the pupal parasitoid *Pimpla (Coccygomimus) turionellae*: an additional solution to the reliability–detectability problem. *Biol. Control* **11**, 141–146.
- Wahl, D. B. 1997 The cladistics of the genera and subgenera of Xoridinae. *Mem. Am. Entomol. Inst.* **57**, 454–460.
- Wahl, D. B. & Gauld, I. D. 1998 The cladistics and higher classification of the Pimpliformes (Hymenoptera: Ichneumonidae). *Syst. Entomol.* **23**, 299–303.
- Whitfield, J. B. 1992 Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera. *J. Hymenopt. Res.* **1**, 3–14.
- Whitfield, J. B. 1998 Phylogeny and evolution of host–parasitoid interactions in Hymenoptera. *A. Rev. Entomol.* **43**, 129–151.
- Williams, G. C. 1992 *Natural selection: domains, levels, and challenges*. New York: Oxford University Press.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.